

## Structure and dynamics of the community of *Cystoseira zosteroides* (Turner) C. Agardh (Fucales, Phaeophyceae) in the northwestern Mediterranean\*

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**SUMMARY:** Research on community structure and dynamics has been carried out in a *Cystoseira zosteroides* community from Tossa de Mar (Northwestern Mediterranean). The Mediterranean endemic *Cystoseira zosteroides* is a rheophilous and sciaphilic species that occurs in reduced areas from the circalittoral zone, always below 15 m depth. *Cystoseira zosteroides* is the dominant species in a widespread association previously described as *Cystoseiretum zosteroidis* by means of phytosociological methods. Other Phaeophyceae such as *Dictyota dichotoma*, *Halopteris filicina* and *Cladostephus hirsutus* are seasonally abundant in the community. Encrusting algae (e.g. *Lithophyllum incrustans*, *Mesophyllum lichenoides*, *Peyssonnelia rosa-marina*) cover the entire substrate and represent a high percentage of the total biomass. Algal biomass ranges between 1250 and 1900 g dwt m<sup>-2</sup> (including calcareous algae) and percentage coverage ranges between 130 and 360 %. Species richness and species diversity are high in comparison with other Mediterranean *Cystoseira* communities; these features have been related to the coexistence of photophilic and sciaphilic algae within the community. Areas of 900 cm<sup>2</sup> are recommended in order to collect representative samples of the community. There is a great structural and functional variation all along the year as it occurs in other Mediterranean phytobenthic communities. The production phase occurs in spring, while the diversification phase occurs in late summer and autumn. Growth of *Cystoseira zosteroides* and other conspicuous algae seems to be mainly limited by light availability in winter, although nutrient availability probably limits growth in summer. A spring growth of primary laterals partially supported by photosynthate translocation from the tophules placed in the bases of such branches is suggested. Annual production of *Cystoseira zosteroides* has been estimated to be 24 g C m<sup>-2</sup> y<sup>-1</sup> and overall community production amounts to 81 g C m<sup>-2</sup> y<sup>-1</sup>. These production values are similar to those obtained in other light-limited phytobenthic communities.

**Key words:** Phytobenthos, *Cystoseira*, community structure, primary production, northwestern Mediterranean.

**RESUMEN:** ESTRUCTURA Y DINÁMICA DE LA COMUNIDAD DE *Cystoseira zosteroides* (TURNER) C. AGARDH (FUCALES, PHAEOPHYCEAE) EN EL MEDITERRÁNEO NOROCCIDENTAL. — Se analiza la composición específica, la estructura y la dinámica de la comunidad de *Cystoseira zosteroides* de Tossa de Mar (Mediterráneo noroccidental). *Cystoseira zosteroides*, endémica en el Mediterráneo, es una especie reófila y esciáfila que aparece en áreas muy concretas de la zona circalitoral, siempre por debajo de los 15 metros de profundidad. Es la especie dominante del *Cystoseiretum zosteroidis*, una asociación ampliamente extendida por todo el Mediterráneo occidental, previamente descrita mediante métodos fitosociológicos. Otras feofíceas como *Dictyota dichotoma*, *Halopteris filicina* y *Cladostephus hirsutus* son estacionalmente abundantes. Las algas incrustantes (*Lithophyllum incrustans*, *Mesophyllum lichenoides*, *Peyssonnelia rosa-marina*) cubren todo el sustrato disponible y constituyen un elevado porcentaje de la biomasa total. La biomasa algal oscila entre 1250 y 1900 g ps m<sup>-2</sup> (incluyendo las algas calcáreas) y el recubrimiento se sitúa entre el 130 y el 360 %. La riqueza específica y la diversidad son muy elevadas en relación a otras comunidades mediterráneas de *Cystoseira*; esto se ha atribuido a la coexistencia de algas fotófilas y esciáfilas en la comunidad. En base al estudio de las curvas especies/área y diversidad/área, se recomiendan áreas de 900 cm<sup>2</sup> para obtener muestras representativas de la comunidad. Hay una gran variación estructural y funcional a lo largo del año, como ocurre en la mayoría de comunidades fitobentónicas del Mediterráneo. La fase de producción tiene lugar en primavera y la fase de diversificación a finales de verano y en otoño. El crecimiento de *Cystoseira zosteroides* y otras algas conspicuas de la comunidad parece estar limitado por la disponibilidad de luz durante el invierno aunque la baja disponibilidad de nutrientes probablemente es la responsable del escaso crecimiento estival. Sugerimos que el crecimiento primaveral de los ramos está parcialmente mantenido por la translocación de sustancias de reserva desde los tofúlos hacia los ápices. La producción anual de *Cystoseira zosteroides* se ha estimado en 24 g C m<sup>-2</sup> año<sup>-1</sup> y la producción de toda la comunidad alcanza los 81 g C m<sup>-2</sup> año<sup>-1</sup>. Esta producción es parecida a la de otras comunidades fitobentónicas marinas limitadas por la luz.

**Palabras clave:** Fitobentos, *Cystoseira*, estructura, producción primaria, Mediterráneo noroccidental.

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## INTRODUCTION

Data about the floristic composition of the circalittoral rocky bottoms of the Mediterranean Sea is scarce. The main reason for this is the difficulty of direct sampling with SCUBA at depths where circalittoral communities develop. Nevertheless, the structure and dynamics of circalittoral communities deserve attention, not only because of their floristic singularity, very rich in Mediterranean endemics (BOUDOURESQUE, 1973), but because such communities are a paradigmatic example of oligotrophic environments with such low irradiance levels that light usually is the limiting environmental factor for seaweed growth. In the *Cystoseira zosteroides* community, that interest is furthered by the wide bathymetric distribution of the genus *Cystoseira* in Mediterranean waters (GIACCONE & BRUNI, 1973). In previous papers I have studied other *Cystoseira* communities from shallow waters: the *Cystoseira mediterranea* community, from exposed places (BALLESTEROS, 1988a), and the *Cystoseira caespitosa* community from sheltered places (BALLESTEROS, 1990b). The study of the deep water community of *Cystoseira zosteroides* may allow us to find the way the different environmental conditions affect the growth and the species distribution inside the community. *Cystoseira zosteroides* is a perennial species with an erect thallus monopodically organized. It is characterized by the presence of smooth, spaced, subulate, vesicles (tophules) situated at the bases of primary branches, and by the existence of receptacles at the bases of secondary laterals (GIACCONE & BRUNI, 1973) (Fig. 1). *Cystoseira zosteroides* usually appears in the circalittoral zone (BOUDOURESQUE, 1985) but it can occasionally appear in the lower levels of the infralittoral zone if deep water upwellings are regularly present (GIACCONE, 1977). It is distributed throughout the western Mediterranean (GIACCONE, 1970) with the exception of the Alboran Sea and neighbouring areas (GIACCONE, 1974). *Cystoseira zosteroides* is the dominant species in a community described by GIACCONE (1973) and named *Cystoseiretum zosteroidis* which occurs on rocky bottoms exposed to strong unidirectional currents and with light ranging between 1 % and 0.3 % of surface irradiance (GIACCONE & BRUNI, 1973). This association has been described from some areas of the Italian coast (GIACCONE & SORTINO, 1974; BATTIATO *et al.*, 1979), the French coast (FELDMANN, 1937; BOUDOURESQUE, 1973; VERLAQUE, 1987) and the Spanish coast

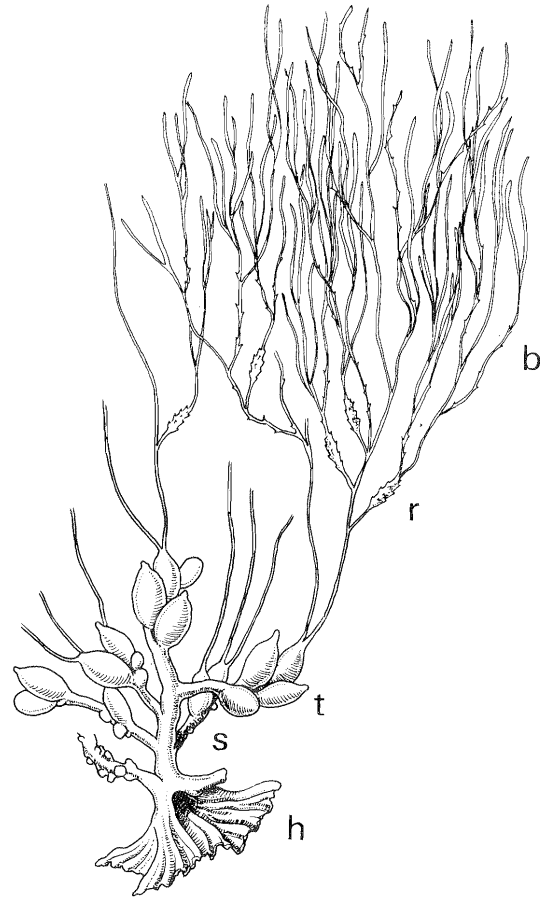


FIG. 1. — Representation of a thallus of *Cystoseira zosteroides* showing holdfast (h), stipe (s), tophules (t), receptacles (r) and branches (b). ( $\times 1$ ) (drawing by J. Corbera)

(BALLESTEROS, 1983; GILI & ROS, 1985; BOISSET & GARCÍA CARRASCOSA, 1987).

The objectives of the present study are:

- To make a quantitative analysis of the *Cystoseiretum zosteroidis*.
- To increase the knowledge of dynamic processes that occur in the *Cystoseiretum zosteroidis*.
- To estimate the primary production of *Cystoseira zosteroides* and other outstanding species in the community.
- To relate structural patterns and functional aspects of the community of *Cystoseira zosteroides* to the environmental factors that can limit seaweed growth at the depths where the community develops.

## MATERIALS AND METHODS

The sampling area is located on a small island off Tossa de Mar (NW Mediterranean,  $41^{\circ} 48' N - 2^{\circ} 26'$

E). Biological and environmental characteristics are extensively commented on by BALLESTEROS (1984). The community of *Cystoseira zosteroides* appears in a reduced area of the bottom situated on the NE slope of the island, between 17 and 19 m depth. It is limited above by the *Codium vermilare* community (BALLESTEROS, 1989a) and below by soft bottoms corresponding to the biocenosis of the coarse sands and fine gravels subject to bottom currents (SGFC) (PÉRES, 1967).

Samples to establish the community structure were taken seasonally (February, May, August, November) by scraping off all organisms (BOUDOURESQUE, 1971) including encrusting algae. Samples were collected as 16 subsamples of  $10 \times 10 \text{ cm}^2$  arranged in a reticulate manner (BALLESTEROS, 1986), which corresponds to a total sampling area of  $1600 \text{ cm}^2$ . Each subsample was carefully sorted in the laboratory. Abundance was quantified as coverage in  $\text{cm}^2$  and biomass (g dwt), using procedures described in BALLESTEROS (1986). Species/abundance matrices were obtained for each sample, with each  $x_{ij}$  representing the biomass (or coverage) of the species  $i$  in the subsample  $j$ . Species/area curves, diversity (Shannon)/area curves, homogeneity/area curves and the variation of the variance: mean ratio for the biomass distribution related to sampled area were computed from these matrices. The following structural parameters, described in BALLESTEROS (1986), were estimated:

- Biomass.
- Coverage.
- Species richness ( $R$ ): the number of species corresponding to the Calleja point  $5 \cdot 10^{-2}$  in the species/area curve.
- Specific distribution ( $k$ ): value of  $k$  defined as

$$k = e^{-b/a}$$

where  $a$  and  $b$  correspond to the slope and the ordinate axis intersection in the species/area curve fitted with a semilogarithmic function

$$y = a \ln x + b$$

where  $y$  is the number of species and  $x$  the area sampled in  $\text{cm}^2$ .

- Molinier 20/5 point (NEDELEC, 1979): the sampling area at which a 20 % increment in sampling area resulted in a 5 % increment in species number. It can be considered as a qualitative minimal area.
- Species diversity ( $A$ ): asymptotic value of diversity when the diversity/area curve is fitted with a Michaelis-Menten function.
- Pattern-diversity ( $S$ ): surface corresponding to the

Calleja point  $1 \cdot 10^{-3}$  in the diversity/area curve fitted with a Michaelis - Menten function. This surface obviously corresponds to the area at which diversity is practically stabilized, so it is related to the structural minimal area.

Species were also qualified by their ecological preferences, and the relative abundances of the main ecological supergroups (BOUDOURESQUE, 1985) were considered to typify the community.

Species terminology follows criteria established by BALLESTEROS (1990b).

Production studies were performed during the year 1983. Branch production of *Cystoseira zosteroides* was estimated by means of their biomass cycle. A sample of  $1600 \text{ cm}^2$  was collected each two months. Thalli of *Cystoseira* were sorted into four compartments of different morphology and turnover: holdfasts, stipes, tophules and branches. Branch biomass was corrected for the average biomass of holdfasts and stipes to estimate population branch biomass, assuming linearity between branch biomass and stipes and holdfast biomass at each sampling period (BALLESTEROS, 1984).

In order to evaluate the production of holdfasts, stipes and tophules, all the thalli of *Cystoseira zosteroides* from an area of  $1600 \text{ cm}^2$  were tagged. Tophules of each thallus were counted on 9/1/1983 and the 9/1/1984. Tagged thalli were collected and biomass of the different compartments was calculated. Knowing tophules formation in relation to number of tophules, and tophule biomass of the population of *Cystoseira zosteroides*, tophule production per square meter and year can be estimated as

$$P = 6.25 \cdot \frac{[\sum (N_{t2} - N_{t1})]}{N_{t2}} \cdot \sum B_t \cdot f$$

for each  $i$  with  $N_{t2} > N_{t1}$

where

$N_{t2}$  = number of tophules at  $t_2$

$N_{t1}$  = number of tophules at  $t_1$

$B_{t2}$  = biomass of tophules at  $t_2$

$n$  = number of tagged thalli

$f$  = correction factor to convert tophule biomass of the sample to whole population tophule biomass.

The production of holdfasts and stipes was estimated by counting the number of tophule whorls for each tagged thallus. The age of each thallus can easily be estimated by taking into account that a new whorl of tophules is created every summer (pers. obs.). Thus, production of holdfasts and stipes can be estimated as

$$P_{h+s} = 6.25 \cdot \frac{\sum^n (B_{h+s}) \cdot f}{w}$$

where

$B_{h+s}$  = holdfast and stipe biomass

$w$  = number of whorls

$n$  = number of tagged thalli

$f$  = correction factor to convert holdfast and stipes biomass of the sample to the population holdfast and stipes biomass.

The overall production of *Cystoseira zosteroides* has been calculated as the sum of the production of each compartment. Conversion to grams of carbon has been performed from determination of carbon content with a Carlo-Erba Nitrogen Analyzer 1500.

Production of other species can reach similar values to production of *Cystoseira zosteroides*. In order to account for this production we have estimated production minima as functions of the biomass cycle of the different species from the same samples used to estimate the biomass cycle of *Cystoseira zosteroides*. Production of large species with annual vegetative cycles has been considered to be equal to their biomass maxima. Epiphyte production has been estimated as the cumulative biomass of the different samples, because epiphytes renew their biomass every two or three months, as observed from quantitative and qualitative changes in epiphytic assemblages (BALLESTEROS, 1984).

## RESULTS

Quantified species lists are presented in Annex 1. Community structure corresponds, in its developed stage, to the structure of Mediterranean phytobenthic communities dominated by frondose algae (ROS *et al.*, 1984). The layer of erect algae is dominated by *Cystoseira zosteroides* and some individuals of *Cystoseira spinosa*. A few laminar and large branched algae grow above *Cystoseira* or the encrusting algae in spring and summer: *Dictyota dichotoma*, *Halopteris filicina*, *H. scoparia*, *Cladostephus hirsutus*, *Phyllariopsis brevipes*, *Bonnemaisonia asparagoides*, *Dictyopteris membranacea*, *Taonia atomaria* and *Sphaerococcus coronopifolius*. Below these algae are found *Peyssonnelia* species, *Rhodymenia ardisonei*, and some turf algae (*Corallina elongata*, *Jania* species, *Gigartina acicularis*, *Cordylecladia erecta*, *Cladophora hutchinsiae* and *Sphacelaria plumula*) develop. The basal stratum is dominated by an encrusting layer of calcareous algae that has been attributed

to *Lithophyllum incrustans*, which coexists with *Mesophyllum lichenoides* and *Peyssonnelia rosa marina*. Epiphytes are abundantly represented by a high number of Ceramiaceae and Delesseriaceae, and some Ectocarpaceae, Rhodomelaceae, minute Corallinaceae and Rhodymeniales. *Cystoseira zosteroides* can shelter a special epiphytic assemblage with *Elachista neglecta*, *Acinetospora vidovichii* and *Streblospora irritans*, at the end of the spring. The aspect of the community changes through the year. At the beginning of winter, the community is only constituted by the encrusting algae layer, thalli of *Cystoseira zosteroides* devoid of branches, and a few scarcely developed species (*Corallina*, *Gigartina*, *Cordylecladia*). However, the number of species is high because there are a lot of juvenile stages of filamentous and laminar algae. At the end of the winter *Cystoseira* branches begin to grow and a great development of large species with an annual cycle occurs during spring. Some filamentous species (*Falkenbergia rufolanosa*, *Callithamnion* sp., *Crouania attenuata*, *Plocamium cartilagineum*) and laminar algae (*Acrosorium uncinatum*, *Rhodophyllis divaricata*) are highly developed at this period of the year. In early summer, *Cystoseira zosteroides* has a biomass maximum (100-120 g dwt m<sup>-2</sup>) and overall community coverage exceeds 300 %. Erect species biomass also reaches a maximum in early summer (500 g dwt m<sup>-2</sup>). *Cystoseira* branches became progressively covered by *Elachista neglecta* and by minute encrusting Corallinaceae during summer. The species with a spring development gradually disappear, and *Cladostephus hirsutus*, *Halopteris scoparia* and *Jania* species attain biomass maxima. Autumnal storms remove nearly all the annual algae and the branches of

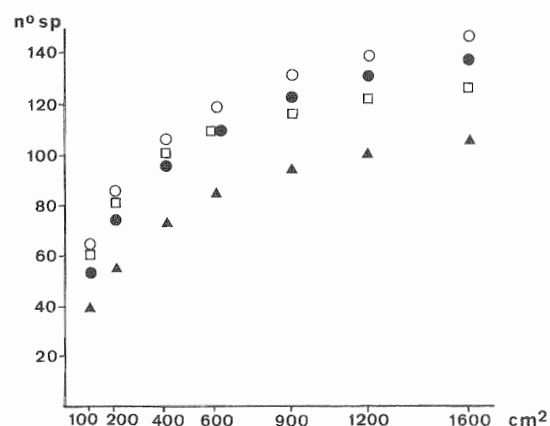


FIG. 2. — Species/area curves in the *Cystoseira zosteroides* community. Different samples are figured with different symbols: winter (220283) (black circles), spring (250582) (white circles), summer (240882) (quadrats) and autumn (141182) (triangles).

TABLE 1. — Seasonal variation in biomass (g dwt m<sup>-2</sup>), percentage coverage, species distribution (*k*), species richness (*R*) and qualitative minimal area (M20/5) for the different samples.

Sample	Biomass	% cov		<i>R</i>	M20/5
220283	1256.3	149.9	18.057	111.8	692
250582	1845.0	359.8	12.643	120.6	485
240882	1822.8	213.8	6.602	102.8	253
141182	1879.8	132.1	21.386	80.6	820

*Cystoseira zosteroides*. At this time, algal coverage is minimal (130 %), as is erect algae biomass (60-110 g dwt m<sup>-2</sup>, a 80 % corresponding to holdfasts and stipes of *Cystoseira zosteroides*).

The species/area curves are represented in figure 2. Species richness is very high and a gradual increase from autumn to spring and a subsequent decline in summer can be observed. Values of *k* are also high, with lower values in summer and higher values in autumn (Table 1).

Species diversity is also high and ranges between 0.6 and 3.5 bits (computed from biomass values) or 2.3 and 4.9 bits (computed from coverage values) (Table 2). Diversity is higher in winter and spring, when species richness is high and evenness is greater because of growth of erect algae that reduce the dominance of encrusting algae. Diversity spectra become stabilized at areas between 120 and 330 cm<sup>2</sup> (Figs. 3, 4). This stabilization occurs at reduced sampling areas in autumn, when the assemblage homogeneity is higher (Figs. 5, 6) and pattern - diversity (*S*) is lower (Table 2). Stabilization occurs at greater sampling areas in winter and spring, coinciding with high values of pattern-diversity. Kulczynski's similarity index stabilizes at areas that range between 400 and 600 cm<sup>2</sup> (Figs. 5, 6), although the spring sample has homogeneity values lower than 0.7 at a sampling area of 800 cm<sup>2</sup>; in this last case, there was a patchy distribution of the dominant erect algae. The great heterogeneity of the spring sample is also detected in the performance of the variance: mean bio-

TABLE 2. — Seasonal variation in species diversity (*A*) and pattern-diversity (*B*) calculated from biomass values (*b*) or coverage values (*r*). Correlation coefficients between experimental and adjusted curves fitted by a Michaelis-Menten function are also indicated.

Sample	<i>Ab</i>	<i>Sb</i>	<i>r</i> <sup>2</sup> <sub><i>b</i></sub>	<i>Ar</i>	<i>Sr</i>	<i>r</i> <sup>2</sup> <sub><i>r</i></sub>
220283	1.94	238	0.939	4.92	325	0.988
250582	3.44	290	0.990	3.89	279	0.992
240882	1.39	173	0.976	3.66	266	0.994
141182	0.64	118	0.956	2.33	252	0.982

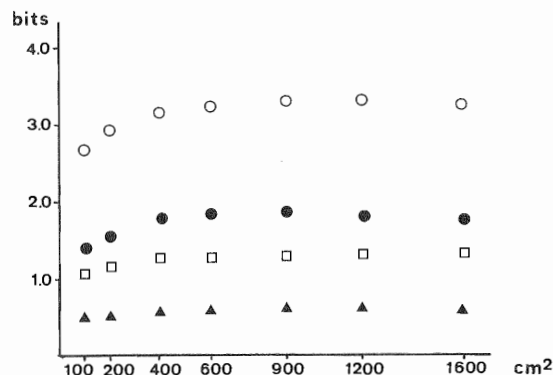


FIG. 3. — Diversity (computed from biomass values)/area curves. Symbols as in figure 2.

mass ratio in function of sampling area (Fig. 7), which is rather high, even for surfaces of 1200 cm<sup>2</sup>.

Sample areas of 900 cm<sup>2</sup> are proposed as suitable for the community at any period of the year because of the great heterogeneity that the community shows in spring and the scattered species distribution within the community in autumn.

Sciaphilic species are dominant (Table 3). Nevertheless, photophilic algae have an unusual importance for a circalittoral community because of their increased coverage in summer months.

Branch production of *Cystoseira zosteroides* is presented in table 4. Production is higher at the beginning of spring but branch growth is maintained until August. Branch production is not detectable from late august to early winter. Production of tophules, holdfasts and stipes has been estimated from data presented in table 5. Tophule production amounts 7.6 g dwt m<sup>-2</sup> y<sup>-1</sup> and the production of holdfasts and stipes is rather lower (3.6 g dwt m<sup>-2</sup> y<sup>-1</sup>). Production of the different compartments is summarized in table 6. The annual biomass cycle of

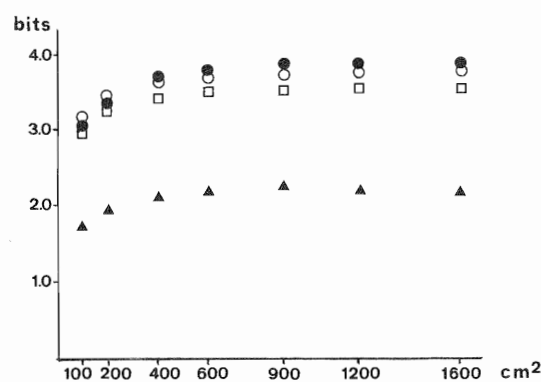


FIG. 4. — Diversity (computed from coverage values)/area curves. Symbols as in figure 2.

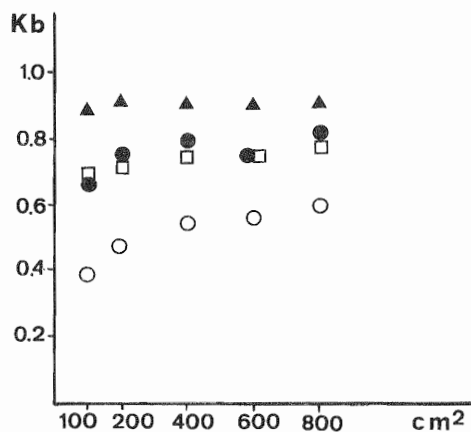


FIG. 5. — Quantitative similarity (computed from biomass values)/area curves. Symbols as in figure 2.

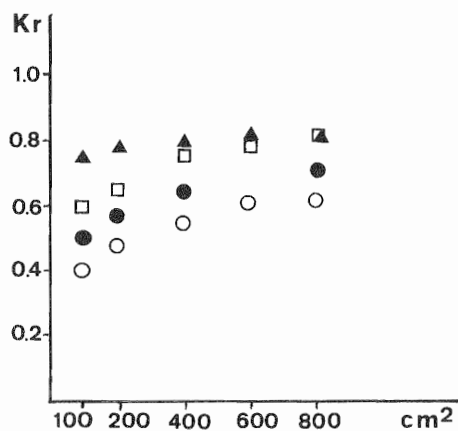


FIG. 6. — Quantitative homogeneity (computed from coverage values)/area curves. Symbols as in figure 2.

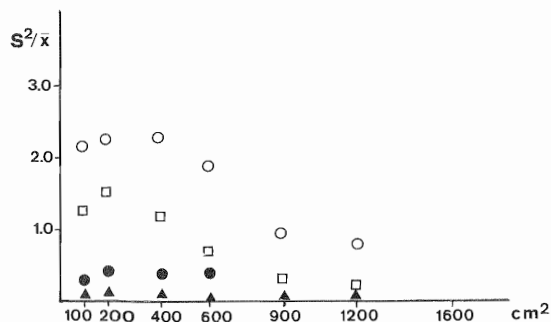


FIG. 7. — Variation of the variance: mean ratio of the biomass distribution in relation to sampling area.

TABLE 3. — Qualitative and quantitative dominance of the main ecological groups.

Ecological group	Qualitative dominance	Quantitative dominance
Sciaphilic	51.0	36.0
Photophilic	15.5	26.3
Infralittoral, hard bottoms	6.5	34.6
Thionitrophilic	2.0	0.3
Mediolittoral	2.5	—
<i>Posidonia</i> leaves	1.5	—
Other	21.0	2.7

TABLE 4. — Production values in  $g\ C\ m^{-2}\ d^{-1}$  (Pday) and P:B ratios for *Cystoseira zosteroides* and for different periods of the year. Time (t) and biomass ( $B_2$ ,  $B_1$ ) are also indicated.

Period	t	$B_2$	$B_1$	P	P day	P/B daily
221282-210283	61	45.3	43.2	2.1	0.034	0.001
220283-220483	59	81.4	45.3	36.1	0.612	0.014
230483-200683	59	96.1	81.4	14.7	0.249	0.003
210683-190883	60	102.1	96.1	6.0	0.100	0.001
200883-161083	58	44.6	102.1	—	—	—
171083-221283	67	43.3	44.6	—	—	—

TABLE 5. — Number of tophules (N), tophule biomass ( $B_t$ ) at  $t_2$ , stipe and holdfast biomass ( $B_{s+h}$ ) at  $t_2$ , number of tophule whorls (w) at  $t_2$ , and estimated production of stipe and holdfast ( $P_{s+h}$ ) between  $t_1$  (9/1/83) and  $t_2$  (9/1/84), for 16 tagged individuals of *Cystoseira zosteroides*.

n.º	$N_t$	$N_p$	$B_{s+h}$	$B_t$	w	$P_{s+h}$
1	13	18	0.511	0.265	10	0.027
2	6	16	0.428	0.257	13	0.020
3	16	19	0.569	0.313	8	0.039
4	15	—	—	—	—	—
5	7	9	0.302	0.140	5	0.028
6	10	10	0.187	0.209	6	0.035
7	8	11	0.328	0.336	6	0.056
8	14	18	0.562	0.309	5	0.062
9	14	15	0.676	0.369	6	0.061
10	11	11	0.582	0.321	10	0.032
11	13	16	0.699	0.439	8	0.055
12	6	4	0.068	0.222	7	0.032
13	10	16	0.382	0.250	10	0.025
14	2	0	0.000	0.058	3	0.019
15	26	26	0.631	0.503	8	0.063
16	6	10	0.279	0.102	7	0.015
Σ	177	199	6.204	4.093		0.569

TABLE 6. — Annual production of the different compartments in *Cystoseira zosteroides*.

Compartment	$g\ dwt\ m^{-2}\ y^{-1}$	$g\ C\ m^{-2}\ y^{-1}$
Branches	58.9	20.3
Tophules	7.6	2.6
Stipes + holdfasts	3.6	1.2
Total	70.1	24.2

TABLE 7. — Annual biomass cycles of the main species in the *Cystoseira zosteroides* community from Tossa de Mar (year 1983).  
Values expressed in g dwt m<sup>-2</sup>.

COMPANION SPECIES	220283	220483	200683	190883	161083	221283
<i>Dictyota dichotoma</i> (Hudson) Lamouroux	1.2	16.1	102.0	13.2	3.6	0.2
<i>Corallina elongata</i> Ellis & Solander	73.6	31.3	17.5	35.4	8.7	1.4
<i>Jania corniculata</i> (L.) Lamouroux	15.8	12.3	5.9	37.5	6.8	1.1
<i>Jania rubens</i> (L.) Lamouroux	5.8	7.0	6.3	20.7	13.5	+
<i>Bonnemaisonia asparagoides</i> (Woodward) C. Agardh	0.4	15.1	0.4	.	+	+
<i>Sphaerococcus coronopifolius</i> Stackhouse	1.0	12.3	+	5.1	+	1.8
<i>Jania longifurca</i> Zanardini	4.3	2.3	.	0.8	11.1	0.2
<i>Halopteris scoparia</i> (L.) Sauvageau	5.8	9.2	0.8	4.7	10.5	4.2
<i>Halopteris filicina</i> (Grateloup) Kützting	6.9	7.8	1.4	5.4	0.8	2.4
<i>Cladostephus hirsutus</i> (L.) Prudhomme van Reine	2.5	0.4	5.1	7.7	0.3	0.9
<i>Taonia atomaria</i> (Woodward) J. Agardh	+	.	6.5	2.4	0.4	.
<i>Peyssonnelia squamaria</i> (Gmelin) Decaisne	1.5	1.7	1.2	6.2	0.6	1.2
<i>Dictyopteris membranacea</i> (Stackhouse) Batters	0.7	1.6	4.7	2.7	0.1	0.1
<i>Phyllariopsis brevipes</i> (C. Agardh) Henry & South	0.1	0.1	2.7	.	.	.
<i>Rhodomenia ardissoni</i> J. Feldmann	0.5	0.9	0.8	2.1	1.4	0.1
<i>Peyssonnelia bornetti</i> Boudouresque & Denizot	0.5	0.9	0.8	2.1	1.4	0.1
<i>Gigartina acicularis</i> (Roth) Lamouroux	+	0.4	0.2	1.6	.	0.1
<i>Gelidium pectinatum</i> Schousboe ex Montagne	0.6	1.3	+	.	0.2	.
<i>Chylocladia verticillata</i> (Lightfoot) Bliding	.	1.3	.	.	.	.
<i>Sporochnus pedunculatus</i> (Hudson) C. Agardh	.	1.2	1.2	.	.	.
<i>Cutleria monoica</i> Ollivier	.	0.2	1.1	.	.	.
<i>Rodriguezella pinnata</i> (Kützting) Schmitz	+	0.8	0.1	0.1	.	+
<i>Halopitys incurvus</i> (Hudson) Batters	.	0.8	+	.	.	.
<i>Cordylecladia erecta</i> (Greville) J. Agardh	+	0.1	+	.	0.5	+
<i>Cryptonemia lomation</i> (Bertolini) J. Agardh	+	0.3	.	+	.	.
<i>Stictyosiphon soriferus</i> (Reinke) Rosenvinge	.	0.2	.	.	.	.
<i>Udotea petiolata</i> (Turra) Boergesen	.	+	.	0.2	.	.
<i>Dasyopsis plana</i> (C. Agardh) Zanardini	+	0.2	+	0.1	+	.
<i>Asperococcus turneri</i> Hooker v. <i>profundus</i> J. Feldmann	.	0.1	0.1	.	.	.
<i>Padina pavonica</i> (L.) Thivy	.	0.1	.	0.1	.	.
Others	+	+	1.4	1.3	0.1	+
EPIPHYTES						
<i>Acinetospora vidovichii</i> (Meneghini) Sauvageau	.	.	11.7	.	.	.
Others	6.9	46.5	4.9	7.1	1.3	1.6

the companion species and epiphytes is presented in table 7. Globally, the production of the community of *Cystoseira zosteroides* can be estimated to amount to 486.1 g dwt m<sup>-2</sup> y<sup>-1</sup>, which approximately equals to 81 g C m<sup>-2</sup> y<sup>-1</sup>. Only 30 % of this production can be attributed to production of the dominant species (24.2 g C m<sup>-2</sup> y<sup>-1</sup>). Epiphyte production accounts for 12 % (10 g C m<sup>-2</sup> y<sup>-1</sup>) and companion species production — mainly *Dictyota dichotoma*, *Bonnemaisonia asparagoides* and some articulated coralline algae — account for the remaining 58 % (47.1 g C m<sup>-2</sup> y<sup>-1</sup>).

## DISCUSSION

The community of *Cystoseira zosteroides* from Tossa de Mar can be included in the association described by GIACONNE (1973). Our samples have a reduced quantitative representation of circalittoral species (with the exception of the dominant species), which can be attributed to the slight depth where samples have been collected. Nevertheless, this rep-

resentation is more significant in qualitative terms, for both the CC group (coralligenous concretion species) (*Rodriguezella pinnata*, *Ceramium diaphanum* v. *Iophophorum*, *Sphondylothamnion multifidum* f. *distichum*, *Myriogramme carnea*, *Gulsonia nodulosa*, *Ceramium bertholdii*, *Didymosporangium repens*) and the SRH group (sciaphilous and rheophilous species) (*Cystoseira zosteroides*, *Phyllariopsis brevipes*, *Asperococcus turneri* v. *profundus*, *Cutleria monoica*, *Sporochnus pedunculatus*) (BOUDOURESQUE, 1985). Also, the dominance of sciaphilic species over photophilic ones is highly significant.

The spatial structure of the *Cystoseira zosteroides* community is similar to other Mediterranean phytobenthic communities dominated by large algae (Table 8). The biomass is similar to biomass values obtained in infralittoral *Cystoseira* communities, although the coverage is slightly lower. The differences may be caused by a greater contribution of encrusting corallines to the overall biomass in deep water. The high average diversity (3.5 bits) is very similar to other infralittoral and circalittoral Mediter-

TABLE 8. — Structural parameters of different infralittoral and circalittoral communities from the Northwestern Mediterranean. Depth (D, in meters), sampling area (S, in cm<sup>2</sup>), N (number of species per sample), species diversity (A<sub>r</sub>, in bits), pattern - diversity (S<sub>r</sub>, in cm<sup>2</sup>), biomass (B, in g dwt m<sup>-2</sup>) and percentage coverage (% cov) are indicated.

Community	D	S	N	A <sub>r</sub>	S <sub>r</sub>	B	% cov.	reference
<i>Cystoseiretum zosteroidis</i>	17.5	1600	132	3.5	281	1424.9	201.4	this study
<i>Cystoseiretum spinosae</i>	20.0	400	68	3.95	—	1381.2	332.8	BALLESTEROS (unpublished data)
<i>Rhodymenio-Codietum vermicularae</i>	11.0	1024	123	3.9	246	1809.7	304.9	BALLESTEROS (1989a)
<i>Rhodymenio-Codietum vermicularae</i>	10	400	38	—	—	2022.6	—	PERERA (1986)
<i>Halimedo-Mesophylletum lichenoidis</i>	17.5	1024	76	2.5	156	1648.1	263.1	BALLESTEROS (in press)
<i>Peyssonnelietum rubrae</i>	variable	600	38	3.2	—	—	157.9	BOUDOURESQUE (1973)
<i>Udoteo-Peyssonnelietum</i>	variable	400	37	3.3	—	—	148.6	BOISSET & GARCÍA CARRASCOSA (1987)
<i>Cystoseiretum caespitosae</i>	0.4	784	105	3.5	186	1438.8	499.0	BALLESTEROS (1990a)
<i>Cystoseiretum balearicae</i>	5.0	250	84	3.6	—	—	246.7	VERLAQUE (1987)
<i>Padino-Cladostephetum hirsutae</i>	3.0	784	104	3.4	177	2085.2	357.8	BALLESTEROS (1984)

anean communities (Table 8). The number of species is surprisingly high, and the average of 132 species per sample is the highest species richness ever reported for Mediterranean phytobenthic communities (BALLESTEROS, 1984). The coexistence of so many algal species in this community may be attributed to the particular light conditions which allow the growth of both sciaphilous and photophilic species. In fact, the community of *Cystoseira zosteroides* behaves as an ecotone between the circalittoral and the infralittoral zones. The high values of parameters related to pattern-diversity ( $k$ ,  $S$ ), are partially conditioned by this high species richness, but mainly caused by the scattered spatial distribution of the species. The relative lack of light prevents high coverages and, also, a concentrated distribution of species in reduced areas. Likewise, the abundance of species other than *Cystoseira zosteroides* — at least during spring and summer — increases pattern-diversity.

Community dynamics can be included in the model described by BALLESTEROS (1990c) for Mediterranean phytobenthic communities. Highest diversities are attained during the period of diversified community (winter) coinciding with high species richness and a scattered spatial distribution of species (Tables 1 and 2). The high diversity also obtained in the developed community is unusual in phytobenthic communities (BALLESTEROS, 1988a, b; 1989b, 1990a) and is caused by the codominance of *Cystoseira zosteroides* with other species.

The production phase occurs in spring and early summer and the diversification phase occurs in autumn-winter. Production values of *Cystoseira zosteroides* are much lower than production values obtained for other *Cystoseira* species inhabiting shallow waters (BALLESTEROS, 1988a, 1990a).

Growth of *Cystoseira zosteroides* is highest at the beginning of spring when branch growth attains 0.6 g dwt m<sup>-2</sup> d<sup>-1</sup> (Table 5). The P:B ratio is also maximum at this period. These high values of branch growth and P:B ratio coincide with relatively high nitrate concentrations in seawater and very low irradiance levels (2-4 W m<sup>-2</sup>) (Fig. 8). Although data on photosynthesis or growth vs. irradiance is not available for *Cystoseira zosteroides*, other circalittoral Mediterranean algae are photosynthetically saturated at 6 W m<sup>-2</sup> (*Udotea petiolata*) or 23 W m<sup>-2</sup> (*Laminaria ochroleuca*) (DREW & LARKUM, 1967; DREW *et al.*, 1982). Photosynthetic saturation levels obtained in other species of *Cystoseira* from Mediterranean infralittoral communities (TREMBLIN *et al.*, 1986) are very high and cannot be attributed to a circalittoral species, in spite of their great similarity in pigment

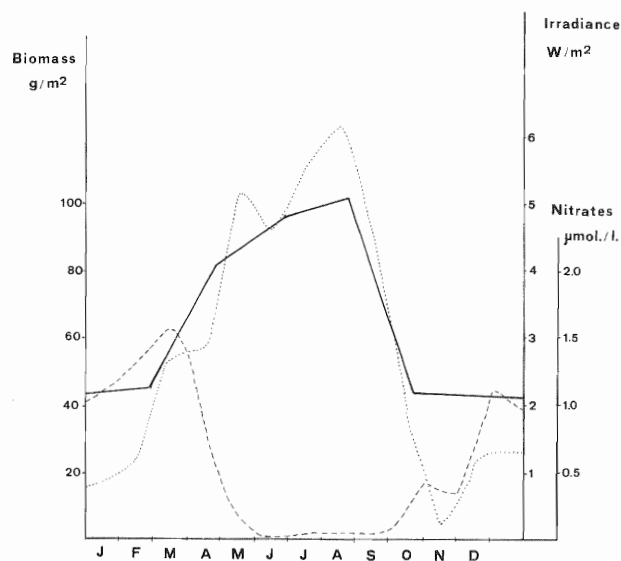


FIG. 8. — Changes in branch biomass of *Cystoseira zosteroides* (continuous line), irradiance (dotted line) and nitrate concentration in seawater (broken line) at 18 meters depth, during the year 1983.



composition (CATALAN & BALLESTEROS, unpublished data). Although we cannot reject the hypothesis that branches of *Cystoseira zosteroides* may have their growth saturated at irradiance values of  $2 \text{ W m}^{-2}$ , such an hypothesis seems very unlikely, and we suggest that the enhanced spring growth may be partially sustained by photosynthetates stored in the tophules during the summer (COMBAUT *et al.*, 1976). The high seawater nitrate concentration in winter (Fig. 8) and the great photosynthetate translocation capacity of *Cystoseira* species bearing tophules (PENOT *et al.*, 1985) suggest that *Cystoseira zosteroides* has a similar strategy to that found in other brown — algae (LUNING, 1971; MANN, 1973; DUNTON & SCHELL, 1986) and seagrasses (ROMERO, 1985), growing in places where high irradiance values do not coincide in time with high nutrient availability. Tophule production during summer (FELDMANN, 1937) would be a mechanism to store photosynthetates when growth is highly limited because of nutrient depletion. Translocation of these photosynthetates to initiate branch growth at the end of the winter would allow *Cystoseira zosteroides* plants to increase their photosynthetic potential when irradiance is high enough to support algal growth. This could be interpreted as a strategy to avoid competition with other algae for light and nutrients. Nevertheless, epiphyte production is also higher at this period of the year (Table 7).

In contrast to what has been found in *Cystoseira mediterranea* (BALLESTEROS, 1988a) and in *Cystoseira caespitosa* (BALLESTEROS, 1990b), branches of *Cystoseira zosteroides* also grow at the beginning of the summer (Fig. 8), in almost nutrient depleted waters. *Cystoseira zosteroides* makes use of the high summer irradiance to maintain reduced growth. The different companion species have a rhythmic production during the year in relation to their ecological preferences. *Corallina elongata* is the only species growing in winter; this is in accordance with the high resistance of *Corallina* to periods of intense disturbance (LITTLER & KAUKER, 1984), but it is surprising irradiance values are usually very low in winter. The sciaphilic species such as *Bonnemaisonia asparagoides*, *Sphaerococcus coronopifolius* and *Halopteris filicina* have their maximum development in spring, while photophilic species (*Halopteris scoparia*, *Clad-*

*dostephus hirsutus*, *Jania* species) have their maximum development in summer. Finally, the annual Phaeophyceae (*Dictyota dichotoma*, *Taonia atomaria*, *Dictyopteris membranacea*, *Phyllariopsis brevipes*) have their maximum growth in spring, coinciding with detectable nitrate concentrations in the water.

Primary production estimates ( $81 \text{ g C m}^{-2} \text{ y}^{-1}$  for the overall community;  $24 \text{ g C m}^{-2} \text{ y}^{-1}$  for *Cystoseira zosteroides*) are greatly exceeded by production values from infralittoral Mediterranean phytobenthic communities, but are higher than production estimates from the circalittoral *Halimeda tuna* community, usually found in deeper waters (BALLESTEROS, 1984). In comparison with production values from phytobenthic communities from other areas, these production values are similar to those obtained for light-limited species and communities (CHAPMAN & LINDLEY, 1981; DREW *et al.*, 1982; LITTLER *et al.*, 1986; WOLANSKI *et al.*, 1988).

Light availability seems to be a determinant factor in the structure and dynamics of the *Cystoseira zosteroides* community. The high species richness has been attributed to the coexistence of photophilic and sciaphilic algae. The high pattern-diversity and the low coverage are probably caused by the relatively low irradiance that does not permit a high density of species and biomass. Functionally, the *Cystoseira zosteroides* community can be considered to be light-dependent (BALLESTEROS, 1989b) because production is maintained during the summer in spite of almost undetectable nutrient levels in the water. The coexistence of photophilic and sciaphilic species already commented — each group with a different production period — increases the extensive production phase of the community. Nevertheless, nutrient availability seems to limit production and, as has been already demonstrated by COMBAUT *et al.* (1976), photosynthetate translocation from the tophules would allow branch growth of *Cystoseira zosteroides* in early spring, when nutrient concentration is rather high but irradiance may be not sufficient to saturate photosynthesis. Nutrient storage in winter to facilitate branch growth in summer, as occurs in other brown algae (CHAPMAN & GRAIGIE, 1977; MANN *et al.*, 1980), although possible, has not been demonstrated.

ANNEX 1. — Seasonal variation in the species composition of the *Cystoseira zosteroides* community. Species abundance is expressed in percentage coverage (first quantity) and g dwt m<sup>-2</sup> (second quantity). Symbol + means presence (biomass lower than 0.1 gdw m<sup>-2</sup> and coverage lower than 0.1 %).

	220283	220582	240882	141182
<i>Lithophyllum incrustans</i> Philippi	47.2	55.4	84.4	92.4
	887.8	1227.0	1450.1	1749.2
<i>Cystoseira zosteroides</i> (Turner)	6.1	82.4	14.4	5.6
C. Agardh	40.5	111.7	37.4	42.2
<i>Dictyota dichotoma</i> (Hudson)	2.7	78.9	7.7	0.9
Lamouroux	1.2	20.1	7.0	0.4
<i>Corallina elongata</i> Ellis & Solander	20.9	14.5	3.9	3.4
	73.6	57.4	17.8	13.3
<i>Mesophyllum lichenoides</i> (Ellis)	10.1	18.6	2.4	1.6
Lemoine	113.5	217.6	24.1	17.6
<i>Halopteris filicina</i> (Grateloup)	6.2	16.0	4.3	1.5
Kützing	6.9	11.0	4.9	1.8
<i>Cladostephus hirsutus</i> (Linné)	1.5	13.6	9.0	3.7
Prud'homme van Reine	2.5	16.6	16.0	4.7
<i>Halopteris scoparia</i> (Linné)	5.4	2.3	16.4	3.0
Sauvageau	5.8	3.0	20.1	3.6
<i>Jania rubens</i> (Linné) Lamouroux	2.5	4.6	16.0	1.2
	4.3	7.5	23.3	2.0
<i>Jania corniculata</i> (Linné)	9.3	7.3	2.8	0.8
Lamouroux	15.8	11.4	3.9	1.1
<i>Peyssonnelia rosa-marina</i> Boud. & Den. f. <i>saxicola</i> Boud. & Den.	6.2	1.7	9.6	1.8
<i>Elachista neglecta</i> Kuckuck	.	0.8	14.3	.
	.	0.8	17.3	.
<i>Aglaozonia chilosa</i> Falkenberg-phase	4.0	2.7	3.3	3.6
	3.6	3.3	3.1	2.9
Melobesiae unidentified	3.7	2.1	4.4	2.9
	3.7	2.1	4.4	2.9
<i>Acrosorium uncinatum</i> (Turner)	6.1	3.5	.	0.3
Kylin v. <i>venulosum</i> (Zanardini)	1.8	1.3	.	0.1
Boudouresque <i>et al.</i>				
<i>Jania cf. longifurca</i> Zanardini	1.3	2.2	2.6	1.5
	4.3	5.7	7.7	3.4
<i>Rhodymenia ardissonaei</i>	0.7	5.5	0.8	0.1
J. Feldmann	0.7	4.4	0.8	0.1
<i>Callithamnion byssoides</i> Arnott	0.5	4.7	0.1	0.1
ex Harvey	0.5	4.7	0.1	0.1
<i>Phyllariopsis brevipes</i> Henry & South	0.3	4.8	.	.
	0.2	1.5	.	.
<i>Cladophora hutchinsiae</i>	0.4	1.2	1.3	1.0
(Dillwyn) Kützing	0.4	1.8	1.3	1.0
<i>Giffordia mitchelliae</i> (Harvey)	0.1	3.5	+	.
Hamel	0.1	3.5	+	.
<i>Bonnemaisonia asparagoides</i>	0.7	2.9	.	+
(Woodward) C. Agardh	0.6	1.9	.	+
<i>Lithophyllum expansum</i> Philippi	0.1	3.5	.	.
sensu Lemoine	1.6	90.0	.	.
<i>Dictyopteris membranacea</i>	1.4	1.2	0.4	0.1
(Stackhouse) Batters	0.8	0.5	0.4	0.1
<i>Dasya corymbifera</i> J. Agardh	0.4	2.2	0.1	0.1
	0.4	2.2	0.1	0.1
<i>Falkenbergia rufolanosa</i>	0.8	1.6	0.1	0.1
(Harvey) Schmitz-phase	0.8	1.6	0.1	0.1
<i>Sphacelaria cirrosa</i> (Roth)	0.1	1.2	0.9	0.3
C. Agardh	0.1	1.4	0.9	0.3
<i>Gigartina acicularis</i> (Roth)	+	0.8	1.4	0.2
Lamouroux	+	1.0	2.2	0.2
<i>Sphacelaria plumula</i> Zanardini	0.2	0.5	1.6	0.1
	0.2	0.5	1.6	0.1
<i>Seirospora interrupta</i> (Smith)	0.1	2.2	0.1	.
Schmidt	0.1	2.2	0.1	.
<i>Taonia atomaria</i> (Woodward)	+	0.9	1.1	.
J. Agardh	+	0.7	2.9	.
<i>Peyssonnelia squamaria</i> (Gmelin)	0.8	0.3	0.7	.
Decaisne	1.5	0.9	1.5	.
<i>Wrangelia penicillata</i> C. Agardh	0.6	0.5	0.6	0.1
	0.6	0.4	0.6	0.1
<i>Cystoseira spinosa</i> Sauvageau	.	.	.	1.6
	.	.	.	10.5

	220283	220582	240882	141182
<i>Cordylecladia erecta</i> (Greville)	0.1	0.1	0.1	1.2
J. Agardh	0.1	0.1	0.1	1.9
<i>Herposiphonia tenella</i>	0.1	0.1	0.1	1.2
(C. Agardh) Ambrogn v.	0.1	0.1	0.1	1.9
<i>secunda</i> (C. Agardh) Hollenberg				
<i>Callithamnion</i> sp	0.2	1.3	+	.
	0.2	1.3	+	.
<i>Champia parvula</i> (C. Agardh)	0.3	0.6	0.3	0.1
Harvey	0.3	0.5	0.3	0.1
<i>Crouania attenuata</i> (C. Agardh)	0.2	0.8	0.1	0.1
J. Agardh	0.2	0.8	0.1	0.1
<i>Erythroglossum sandrianum</i>	.	1.2	+	.
(Zanardini) Kylin	.	0.4	+	.
<i>Haraldia lenormandii</i> (Derbès & Solier) J. Feldmann	0.1	1.0	.	.
	+	0.3	.	.
<i>Apoglossum ruscifolium</i> (Turner)	0.2	0.5	0.3	+
J. Agardh	0.1	0.2	0.1	+
<i>Gelidium pectinatum</i> Schousboe	0.3	0.5	+	0.1
ex Montagne	0.6	0.8	+	0.1
<i>Plocamium cartilagineum</i> (Linné)	0.4	0.3	0.1	0.1
Dixon	0.4	0.3	0.1	0.1
<i>Rodriguezella pinnata</i> (Kützing)	0.2	0.4	0.2	0.1
Schmitz	0.2	0.4	0.2	0.1
<i>Cladophora prolifera</i> (Roth)	0.1	.	0.6	0.2
Kützing	0.1	.	0.6	0.2
<i>Cystoseira</i> sp.	0.9	.	.	.
	7.0	.	.	.
<i>Pterothamnion crispum</i>	0.3	0.4	+	+
(Ducluzeau) Nägeli	0.3	0.2	+	+
<i>Corallina granifera</i> Ellis & Solander	+	0.4	0.1	0.2
	+	0.8	0.2	0.3
<i>Pterothamnion plumula</i> (Ellis)	0.5	0.1	+	0.1
Nägeli v. <i>bebbii</i> (Reinsch)	0.5	0.1	+	0.1
J. Feldmann				
<i>Rhodophyllis divaricata</i>	0.1	0.5	.	0.1
(Stackhouse) Papenfuss	0.1	0.3	.	0.1
<i>Asperococcus turneri</i> (Smith)	.	0.7	.	.
Hooker v. <i>profundus</i>	.	0.3	.	.
J. Feldmann				
<i>Monosporus pedicellatus</i> (Smith)	0.3	0.1	0.1	0.1
Solier	0.3	0.1	0.1	0.1
<i>Antithamnion cruciatum</i>	0.1	0.3	0.1	0.1
(C. Agardh) Nägeli	0.1	0.3	0.1	0.1
<i>Peyssonnelia bornetii</i> Boud. & Den.	0.2	0.4	.	+
	0.9	0.9	.	+
<i>Sphondylothamnion multifidum</i>	0.2	0.3	0.1	.
(Hudson) Nägeli f. <i>distichum</i>	0.2	0.3	0.1	.
G. Feldmann				
<i>Sphaerococcus coronopifolius</i>	0.5	0.1	+	.
Stackhouse	1.0	0.4	+	.
<i>Zanardinia prototypus</i> (Nardo)	0.6	+	.	.
Nardo	0.3	+	.	.
<i>Polysiphonia furcellata</i>	0.2	0.2	0.1	+
(C. Agardh) Harvey	0.2	0.2	0.1	+
<i>Aphanocladia stichidiosa</i> (Funk)	0.1	0.2	0.1	0.1
Ardre	0.1	0.2	0.1	0.1
<i>Dudresnaya verticillata</i>	+	0.5	.	.
(Withering) Le Jolis	+	0.6	.	.
<i>Ceramium diaphanum</i>	0.1	0.2	0.1	+
(Lightfoot) Roth	0.1	0.2	0.1	+
v. <i>lophophorum</i> G. Feldmann				
<i>Lomentaria chylocradiella</i> Funk	0.1	0.1	0.2	+
	0.1	0.1	0.2	+
<i>Ceramium echionotum</i>	+	0.1	0.2	0.1
J. Agardh	+	0.1	0.2	0.1
<i>Peyssonnelia rubra</i> (Greville)	0.2	0.1	.	0.1
J. Agardh	0.4	0.4	.	0.2
<i>Callithamnion decompositum</i>	0.3	+	.	0.1
J. Agardh	0.3	+	.	0.1
<i>Halopitys incurvus</i> (Hudson)	.	.	0.4	+
Batters	.	.	0.4	+
<i>Myriogramme carnea</i>	0.3	0.1	.	.
(Rodríguez) Kylin	0.1	+	.	.
<i>Hypoglossum hypoglossoides</i>	+	0.2	0.2	.

	220283	220582	240882	141182		220283	220582	240882	141182
(Stackhouse) Collins & Harvey	+	0.2	0.1	+	<i>Dasya hutchinsiae</i> Harvey	+	+	0.1	+
<i>Ceramium flaccidum</i> (Kützinger)	+	+	0.3	+		+	+	0.1	+
Ardissone	+	+	0.3	+	<i>Chondria dasyphylla</i>	+	+	0.1	.
<i>Compsothamnion thuyoides</i>	0.1	0.1	+	0.1	(Woodward) C. Agardh	+	+	0.1	.
(Smith) Schmitz	0.1	0.1	+	0.1	<i>Dasya punicea</i> Meneghini	+	.	0.1	+
<i>Gloiocladia furcata</i> (C. Agardh)	0.2	0.1	+	+		+	.	0.1	+
J. Agardh	0.2	0.1	+	+	<i>Antithamnion tenuissimum</i>	0.1	.	+	+
<i>Lomentaria ercegovicii</i> Verlaque	0.1	0.1	0.1	+	(Hauck) Schiffner	0.1	.	+	.
<i>et al.</i>	0.1	0.1	0.1	+	<i>Ceramium cingulatum</i> Weber van	+	0.1	.	+
<i>Lyngbya sordida</i> (Zanardini)	0.1	+	0.1	0.1	Bosse	+	0.1	.	+
Gomont	0.1	+	0.1	0.1	<i>Laurencia obtusa</i> (Hudson)	.	+	0.1	+
Gigartinales unidentified	+	+	0.3	.	Lamoureux	.	+	0.1	+
	+	+	0.4	.	<i>Antithamnionella spirographidis</i>	0.1	+	+	.
<i>Spyridia filamentosa</i> (Wulfen)	.	0.1	0.1	0.1	Schiffner	0.1	+	+	.
Harvey	.	0.1	0.1	0.1	<i>Chaetomorpha aerea</i> (Dillwyn)	+	.	0.1	+
<i>Spermothamnion flabellatum</i>	0.1	0.1	.	0.1	Kützinger	+	.	0.1	+
Bornet	0.1	0.1	.	0.1	<i>Stylonema cornu-cervi</i> Reinsch	+	0.1	.	+
<i>Gelidium pusillum</i> (Stackhouse)	.	+	+	0.3		+	0.1	.	+
Le Jolis	.	+	+	0.4	<i>Calosiphonia vermicularis</i>	+	0.1	.	.
<i>Cladophora lehmanniana</i>	+	.	0.3	.	(J. Agardh) Schmitz	+	0.1	.	.
(Lindenberg) Kützinger	+	.	0.3	.	<i>Lyngbya baculum</i> Gomont	.	+	0.1	.
<i>Castagnea cylindrica</i> Sauvageau	.	0.3	+	.		.	+	0.1	.
	.	0.3	+	.	<i>Seirospora sphaerospora</i>	0.1	+	.	.
<i>Cladophora rupestris</i> (Linné)	.	.	0.2	0.1	J. Feldmann	0.1	+	.	.
Kützinger	.	.	0.2	0.2	<i>Lejolisia mediterranea</i> Bornet	.	.	+	0.1
<i>Choristocarpus tenellus</i> (Kützinger)	.	0.3	.	.		.	.	+	0.1
Zanardini	.	0.3	.	.	<i>Erythrotrichia carnea</i> (Dillwyn)	+	0.1	.	.
<i>Acrosorium uncinatum</i> (Turner)	.	.	0.3	.	J. Agardh	+	0.1	.	.
Kylin v. <i>reptans</i> (Crouan & Crouan) Boud. <i>et al.</i>	.	.	0.1	.	<i>Stylonema alsidii</i> (Zanardini)	+	0.1	.	.
<i>Myriactula rivulariae</i> (Suhr)	.	.	0.3	.	Drew	+	0.1	.	.
J. Feldmann	.	.	0.3	.	<i>Bornetia secundiflora</i>	.	0.1	.	+
<i>Colpomenia</i> sp.	+	+	0.2	+	(J. Agardh) Thuret	.	0.1	.	+
	+	+	0.2	+	<i>Calothrix confervicola</i> (Roth)	.	+	0.1	.
<i>Trailiella intricata</i> Batters-phase	+	0.1	0.1	+	C. Agardh	.	+	0.1	.
	+	0.1	0.1	+	<i>Bryopsis plumosa</i> (Hudson)	0.1	.	.	.
<i>Ceramium codii</i> (Richards)	+	0.1	0.1	+	C. Agardh	0.1	.	.	.
Mazoyer	+	0.1	0.1	+	<i>Amphiroa beauvoisii</i> Lamoureux	0.1	.	.	.
<i>Lophosiphonia scopulorum</i>	0.1	+	0.1	+		0.3	.	.	.
(Harvey) Womersley	0.1	+	0.1	+	<i>Gulsonia nodulosa</i> (Ercegovic)	0.1	.	.	.
<i>Compsothamnion gracillimum</i>	0.1	0.1	+	+	J. Feldmann & G. Feldmann	0.1	.	.	.
De Toni	0.1	0.1	+	+	<i>Cutleria monoica</i> Ollivier	.	0.1	.	.
<i>Pterothamnion pluma</i> (Dillwyn)	+	0.1	+	0.1		.	0.1	.	.
Thuret	+	0.1	+	0.1	<i>Nithophyllum micropunctatum</i>	.	.	0.1	.
<i>Feldmannia globifera</i> (Kützinger)	+	0.2	+	.	Funk	.	.	0.1	.
Hamel	+	0.2	+	.	<i>Herposiphonia tenella</i>	+	+	+	+
<i>Polysiphonia elongata</i> (Hudson)	+	0.1	0.1	.	(C. Agardh) Ambronn	+	+	+	+
Sprengel	+	0.1	0.1	.	<i>Dasyopsis plana</i> (C. Agardh)	+	+	+	+
<i>Botryocladia boergesenii</i>	+	0.1	0.1	.	Zanardini	+	+	+	+
J. Feldmann	+	0.1	0.1	.	<i>Callithamniella tingitana</i> (Bornet)	+	+	+	+
<i>Acrosorium uncinatum</i> (Turner)	+	0.1	.	0.1	G. Feldmann	+	+	+	+
Kylin	+	0.1	.	0.1	<i>Halicystis parvula</i> Schmitz	+	+	+	+
<i>Codium vermilara</i> (Oliv.) Delle	+	0.1	0.1	.		+	+	+	+
Chiaje	+	0.1	0.2	.	<i>Dasyopsis spinella</i> (C. Agardh)	+	+	+	+
<i>Padina pavonica</i> (Linné)	.	0.1	0.1	.	Zanardini	+	+	+	+
Lamoureux	.	0.1	0.1	.	<i>Ceramium rubrum</i> (Hudson)	+	+	+	+
<i>Cryptonemia lomatium</i>	+	.	0.2	.	C. Agardh	+	+	+	+
(Bertoloni) J. Agardh	+	.	0.2	.	<i>Fosliella farinosa</i> (Lamoureux)	+	+	.	+
<i>Callithamnion hookeri</i> (Dillwyn)	+	0.2	.	.	Howe	+	+	.	+
Gray	+	0.2	.	.	<i>Cladophora echinus</i> (Biasoletto)	+	.	+	+
<i>Seirospora giraudyi</i> (Kützinger) De Toni	0.1	0.1	.	.	Kützinger	+	.	+	+
	0.1	0.1	.	.	<i>Ceramium ciliatum</i> (Ellis)	+	+	+	.
<i>Amphiroa cryptarthrodia</i>	0.1	.	0.1	.	Ducluzeau v. <i>robustum</i>	+	+	+	.
Zanardini	0.3	.	0.1	.	(J. Agardh) Mazoyer				
<i>Acetabularia acetabulum</i> (Linné)	.	.	0.2	.	<i>Griffithsia</i> sp?	+	.	+	+
Silva	.	.	0.3	.		+	.	+	+
<i>Rhodophyllis strafforellii</i>	.	.	0.2	.	<i>Pleonosporium borneri</i> (Smith)	+	+	+	.
Ardissone	.	.	0.1	.	Hauck	+	+	+	.
<i>Polysiphonia foetidissima</i> Cocks	+	0.1	+	+	<i>Gelidiella</i> sp.	.	+	+	+
	+	0.1	+	+		.	+	+	+
<i>Pterothamnion plumula</i> (Ellis)	0.1	+	+	+	Cladophoraceae ind.	+	+	+	.
Nägeli	0.1	+	+	+		+	+	+	.
<i>Spermothamnion repens</i>	0.1	+	+	+	<i>Griffithsia schousboei</i> Montagne	+	+	+	.
(Dillwyn) Rosenvinge	0.1	+	+	+		+	+	+	.

	220283	220582	240882	141182
<i>Phaeophila viridis</i> (Reinke)	.	+	+	+
Parke & Burrows	.	+	+	+
<i>Derbesia tenuissima</i> (De Notaris)	+	+	.	+
Crouan & Crouan	+	+	.	+
<i>Anotrichium barbatum</i> (Smith)	+	+	+	.
Nägeli	+	+	+	.
<i>Cladophora albida</i> (Hudson)	+	+	+	.
Kützing	+	+	+	.
<i>Spermothamnion</i> sp.	.	+	+	+
	.	+	+	+
<i>Ceramium cinnabarinum</i>	+	+	+	.
(J. Agardh) Hauck	+	+	+	.
<i>Audouinella daviesii</i> (Dillwyn)	+	+	.	.
Woelkerling	+	+	.	.
<i>Lyngbya meneghiniana</i> Gomont	+	.	.	+
	+	.	.	+
<i>Ceramium strictum</i> Harvey	+	.	.	+
	+	.	.	+
<i>Polysiphonia fruticulosa</i>	.	+	.	+
(Wulfen) Sprengel	.	+	.	+
<i>Audouinella caespitosa</i>	+	+	.	.
(J. Agardh) Dixon	+	+	.	.
<i>Bryopsis monoica</i> Berthold	+	.	+	.
	+	.	+	.
<i>Pterosiphonia parasitica</i>	.	+	+	.
(Hudson) Falkenberg	.	+	+	.
<i>Pseudochlorodesmis furcellata</i>	.	+	+	.
(Zanardini) Boergesen	.	+	+	.
<i>Choreonema thuretii</i> (Bornet)	.	.	+	+
Schmitz	.	.	+	+
<i>Nereia filiformis</i> (J. Agardh)	+	+	.	.
Zanardini	+	+	.	.
<i>Antithamnionella elegans</i>	.	+	.	+
(Berthold) Price & John	.	+	.	+
<i>Myriactula gracilis</i> Van der Ben	+	.	+	.
	+	.	+	.
<i>Pringsheimiella scutata</i> (Reinke)	+	+	.	.
Marchewianka	+	+	.	.
<i>Antithamnion heterocladum</i> Funk	+	+	.	.
	+	+	.	.
<i>Enteromorpha</i> sp.	+	+	.	.
	+	+	.	.
Ectocarpaceae unidentified	+	+	.	.
	+	+	.	.
Rhodymeniaceae unidentified?	.	+	.	+
	.	+	.	+
Ceramaceae unidentified	.	.	+	+
	.	.	+	+
<i>Ceramium</i> sp.	+	.	.	.
	+	.	.	.
<i>Pterosiphonia pennata</i>	+	.	.	.
(C. Agardh) Falkenberg	+	.	.	.
<i>Cladophora dalmatica</i> Kützing	+	.	.	.
	+	.	.	.
<i>Ceramium bertholdii</i> Funk	+	.	.	.
	+	.	.	.
<i>Didymosporangium repens</i>	+	.	.	.
Lambert	+	.	.	.
<i>Chaetomorpha</i> sp.	+	.	.	.
	+	.	.	.
<i>Porphyra</i> sp.	+	.	.	.
	+	.	.	.
<i>Myriactula stellulata</i> (Harvey)	.	+	.	.
Levring	.	+	.	.
<i>Peyssonnelia crispata</i> Boud. & Den.	.	+	.	.
	.	+	.	.
<i>Dasya ocellata</i> (Grateloup)	.	+	.	.
Harvey	.	+	.	.
<i>Chaetomorpha capillaris</i>	.	+	.	.
(Kützing) Boergesen	.	+	.	.
<i>Audouinella microscopica</i>	.	+	.	.
(Nägeli) Woelkerling	.	+	.	.

	220283	220582	240882	141182
<i>Chondria coerulescens</i>	.	+	.	.
(J. Agardh) Falkenberg	.	+	.	.
<i>Radicilingua reptans</i> (Kyllin)	.	+	.	.
Papenfuss	.	+	.	.
<i>Callithamnion corymbosum</i>	.	+	.	.
(Smith) Lyngbye	.	+	.	.
<i>Giffordia</i> sp.	.	+	.	.
	.	+	.	.
<i>Stictyosiphon soriferus</i> (Reinke)	.	+	.	.
Rosenvinge	.	+	.	.
<i>Polysiphonia macrocarpa</i> Harvey	.	+	.	.
	.	+	.	.
Bryopsidaceae unidentified	.	+	.	.
	.	+	.	.
<i>Chondria tenuissima</i>	.	.	+	.
(Goodenough & Woodward)	.	.	+	.
C. Agardh	.	.	+	.
<i>Giraudia sphacelarioides</i> Derbès	.	.	+	.
& Solier	.	.	+	.
<i>Enteromorpha clathrata</i> (Roth)	.	.	+	.
Greville	.	.	+	.
<i>Hymenoclonium serpens</i> (Crouan	.	.	+	.
& Crouan) Batters phase	.	.	+	.
<i>Enteromorpha flexuosa</i> (Wulfen	.	.	+	.
ex Roth) J. Agardh	.	.	+	.
<i>Dilophus fasciola</i> (Roth) Howe	.	.	+	.
	.	.	+	.
<i>Heterosiphonia crispella</i>	.	.	+	.
(C. Agardh) Wynne	.	.	+	.
<i>Enteromorpha multiramosa</i>	.	.	+	.
Bliding	.	.	+	.
Rhodomelaceae unidentified	.	.	+	.
	.	.	+	.
<i>Pterocladia capillacea</i> (Gmelin)	.	.	.	+
Bornet & Thuret	.	.	.	+
Nithophylleae unidentified	.	.	.	+
	.	.	.	+
<i>Amphiroa</i> sp.	.	.	.	+
	.	.	.	+
<i>Valonia utricularis</i> (Roth)	.	.	.	+
C. Agardh	.	.	.	+
<i>Polysiphonia opaca</i> (C. Agardh)	.	.	.	+
Morris & De Notaris	.	.	.	+
<i>Halodictyon mirabile</i> Zanardini	.	.	.	+
	.	.	.	+
<i>Rodriguezella</i> sp.?	.	.	.	+
	.	.	.	+

## BIBLIOGRAPHY

- BALLESTEROS, E. — 1983. Contribució al coneixement algològic de la Mediterrània espanyola, III. Addicions a la flora de Tossa de Mar (Girona). *Coll. Bot.*, 14: 43-53.
- 1984. *Els vegetals i la zonació litoral: espècies, comunitats i factors que influeixen en la seva distribució*. Tesis Doctoral. Universitat de Barcelona. 587 pp.
- 1986. Métodos de análisis estructural en comunidades naturales, en particular del fitobentos. *Oecol. Aquat.*, 8: 117-131.
- 1988a. Estructura y dinámica de la comunidad de *Cystoseira mediterranea* Sauvageau en el Mediterráneo noroccidental. *Inv. Pesq.*, 52(3): 313-334.
- 1988b. Composición y estructura de la comunidad infralitoral de *Corallina elongata* Ellis & Solander de la Costa Brava (Mediterráneo Noroccidental). *Inv. Pesq.*, 52(1): 135-151.
- 1989a. Estructura y dinámica de la comunidad infralitoral de *Codium vermilara* (Oliv.) Delle Chiaje de la Costa Brava (Mediterráneo Noroccidental). *Anal. Biol.*, 15: 73-90.

- 1989b. Poduction of seaweeds in Northwestern Mediterranean marine communities: its relation with environmental factors. *Scient. Mar.*, 53(2-3): 357-364.
- 1990a. Structure and dynamics of Northwestern Mediterranean phytobenthic communities: a conceptual model. *Oecol. Aquat.*, 10.
- 1990b. Structure and dynamics of the *Cystoseira caespitosa* Sauvageau (Fucales, Phacophyceae) community in the northwestern Mediterranean. *Scient. Mar.*, 54 (2): 155-168.
- 1990c. Check-list of benthic marine algae from Catalonia (Northwestern Mediterranean). *Treb. Inst. Bot. Barcelona*, 13: 1-52.
- in press. Structure of a deep water community of *Halimeda tuna* from the Northwestern Mediterranean. *Coll. Bot.*
- BATTIATO, A., M. CORMACI, G. FURNARI & B. SCAMMACA. — 1979. Osservazioni sulla zonazione dei popolamenti fitobentonici di substrato duro delle penisole della Maddalena (Siracusa). *Thal. Salentina*, 9: 19-25.
- BOISSET, F. & A. M. GARCÍA CARRASCOSA. — 1987. El fitobentos de las islas Columbretes: flora y comunidades vegetales. In: L. A. ALONSO, J. L. CARRETERO & A. M. GARCÍA CARRASCOSA (eds.), *Islas Columbretes: contribución al estudio de su medio natural*: 269-301. Generalitat Valenciana. Valencia.
- BOUDOURESQUE, C. F. — 1971. Méthodes d'étude qualitative et quantitative du benthos (en particulier du phytobenthos). *Téthys*, 3(1): 79-104.
- 1973. Recherches de bionomie analytique, structurale et expérimentale sur les peuplements benthiques sciaphiles de Méditerranée Occidentale (fraction algale). Les peuplements sciaphiles de mode relativement calme sur substrats durs. *Bull. Mus. Hist. Nat. Marseille*, 33: 147-225.
- 1985. Groupes écologiques d'algues marines et phytocoenoses benthiques en Méditerranée Occidentale: une revue, *Giorn. Bot. Ital.*, 118: 7-42.
- COMBAUT, G., Y. BRUNEAU, G. JEANTY, C. FRANCISCO, J. TESTE & L. CODOMIER. — 1976. Contribution chimique à l'étude de certains aspects biologiques d'une pheophycée de profondeur *Cystoseira zosteroides* (Turn.) C. Ag., *Phycologia*, 15: 275-282.
- CHAPMAN, A. R. O. & J. S. GRAIGIE. — 1977. Seasonal growth on *Laminaria longicruris*: relations with dissolved inorganic nutrients and internal reserves of nitrogen. *Mar. Biol.*, 40: 197-205.
- CHAPMAN, A. R. O. & J. E. LINDLEY. — 1981. Productivity of *Laminaria solidungula* J. Ag. in the Canadian high Arctic: a year round study. In: T. LEVRING (ed.), *Proceed. Xth int. Seaweed Symp.*: 245-258.
- DREW, E. & A. W. D. LARKUM. — 1967. Photosynthesis and growth of *Udotea*, a green alga from deep water. *Under. Ass. Report*: 65-71.
- DREW, E., J. F. IRELAND, C. MUIR, W. A. ROBERTSON & J. D. ROBINSON. — 1982. Photosynthesis, respiration and other factors influencing the growth of *Laminaria ochroleuca* Pyl. below 50 metres in the Strait of Messina. *Mar. Ecol.*, 3(4): 335-355.
- DUNTON, K. H. & D. M. SCHELL. — 1986. Seasonal carbon budget and growth of *Laminaria solidungula* in the Alaskan high Arctic. *Mar. Ecol. Progr. Ser.*, 31: 57-66.
- FELDMANN, J. — 1937. *Recherches sur la végétation marine de la Méditerranée. La côte des Albères*. Wolf. Rouen. 339 pp.
- GIACCONE, G. — 1970. Aspetto di fitocenosi marine del Mediterraneo in presenza di fattori idrodinamici. *Pubbl. Staz. Zool. Napoli*, 38: 34-42.
- 1973. Ecologie et chorologie des *Cystoseira* en Méditerranée. *Rapp. Comm. int. Mer Médit.*, 22(4): 49-50.
- 1974. Tipologia delle comunità fitobentoniche del Mediterraneo. *Mem. Biol. Mar. Oceanogr.*, 4(4-6): 149-160.
- 1977. Significato bionomico delle comunità fotofile e sciafile nel sistema fitale del Mediterraneo. *Atti. IX Congr. Nat. Soc. Ital. Biol. Mar.*: 277-283.
- GIACCONE, G. & A. BRUNI. — 1973. Le *Cystoseira* e la vegetazione sommersa del Mediterraneo. *Atti. Ist. Ven. Sci. Lett. Art.*, 131: 59-103.
- GIACCONE, G. & M. SORTINO. — 1974. Zonazione della vegetazione marina delle isole Egadi (Canale di Sicilia). *Lav. Ist. Bot. Giard. Col. Palermo*, 25: 166-183.
- GILI, J. M. & J. ROS. — 1985. Study and cartography of the benthic communities of Medes Islands (NE Spain). *Mar. Ecol.*, 6(3): 219-238.
- LITTLER, M. M. & B. J. KAUKER. — 1984. Heterotrichy and survival strategies in the red alga *Corallina officinalis* L. *Bot. Mar.*, 27: 37-44.
- LITTLER, M. M., D. S. LITTLER, S. M. BLAIR & J. N. NORRIS. — 1986. Deep water plant communities from an uncharted seamount off San Salvador Island, Bahamas: distribution, abundance and primary productivity. *Deep Sea Res.*, 33(7): 881-892.
- LUNING, K. — 1971. Seasonal growth of *Laminaria hyperborea* under recorded underwater light conditions near Helgoland. In: J. CRISP (ed.), *IVth Europ. Mar. Biol. Symp.*: 347-361. Cambridge University. New York.
- MANN, K. H. — 1973. Seaweeds: their productivity and strategy for growth. *Science*, 182: 978-981.
- MANN, K. H., A. R. O. CHAPMAN & J. A. GAGNÉ. — 1980. Productivity of seaweeds: the potential and the reality. In: P. G. FALKOWSKI (ed.), *Primary productivity in the sea*: 363-380. Plenum. New York.
- NÉDELEC, H. — 1979. *Étude structurale et problèmes d'échantillonnage dans une phytocoénose portuaire*. Mém. Univ. P. et M. Curie, Marseille Luminy. 71 pp.
- PENOT, M., J. DUNAY & M. PELLEGRINI. — 1985. Contribution à l'étude de la fixation et transport du <sup>14</sup>C chez *Cystoseira nodicaulis* (Fucales, Cystoseiraceae). *Phycologia*, 24(1): 93-102.
- PERERA, M. — 1986. *Aproximació a l'estudi sistemàtic i ecològic de les algues bentòniques i litorals del Cap de Creus*. Tesis de Llicenciatura. Universitat de Barcelona. 198 pp.
- PÉRES, J. — 1967. The Mediterranean benthos. *Oceanogr. Mar. Biol. Ann. Rev.*, 5: 449-533.
- ROMERO, J. — 1985. *Estudio ecológico de las fanerógamas marinas de la costa catalana: producción primaria de Posidonia oceanica (L.) Delile en las islas Medas*. Tesis Doctoral. Universidad de Barcelona.
- ROS, J., J. ROMERO, E. BALLESTEROS & J. M. GILI. — 1984. Diving in blue water: the benthos. In: R. MARGALEF (ed.), *The Western Mediterranean*: 233-295. Pergamon. Oxford.
- TREMBLIN, G., A. COUDRET & A. BAGHDADLI. — 1986. Photosynthèse apparente et installation chez deux *Cystoseires* méditerranéennes: *Cystoseira stricta* et *Cystoseira crinita* (Phéophycées, Fucales): effects de la lumière, de la température et de la salinité. *Cryptog. Algol.*, 7(4): 291-300.
- VERLAQUE, M. — 1987. *Contribution à l'étude du phytobenthos d'un écosystème photophile thermophile de Méditerranée Occidentale*. Thèse. Université d'Aix-Marseille.
- WOLANSKI, E., E. DREW, K. M. ABEL & J. O'BRIEN. — 1988. Tidal jets, nutrient upwelling and their influence on the productivity of the alga *Halimeda* in the Ribbon Reefs, Great Barrier Reef. *Est. Coast. Shelf Sci.*, 26: 169-201.

Scient. ed. J. M. Gili